

# Sex differences in spatial cognition in an invertebrate: the cuttlefish

Christelle Jozet-Alves<sup>1,2</sup>, Julien Modéran<sup>1,2</sup> and Ludovic Dickel<sup>1,2,\*</sup>

<sup>1</sup>Groupe Mémoire et Plasticité comportementale, Université de Caen, 14032 Caen cedex, France

<sup>2</sup>Centre de Recherches en Environnement Côtier, Université de Caen, 54 rue du Dr. Charcot, 14530 Luc-sur-Mer, France

Evidence of sex differences in spatial cognition have been reported in a wide range of vertebrate species. Several evolutionary hypotheses have been proposed to explain these differences. The one best supported is the range size hypothesis that links spatial ability to range size. Our study aimed to determine whether male cuttlefish (*Sepia officinalis*; cephalopod mollusc) range over a larger area than females and whether this difference is associated with a cognitive dimorphism in orientation abilities. First, we assessed the distance travelled by sexually immature and mature cuttlefish of both sexes when placed in an open field (test 1). Second, cuttlefish were trained to solve a spatial task in a T-maze, and the spatial strategy preferentially used (right/left turn or visual cues) was determined (test 2). Our results showed that sexually mature males travelled a longer distance in test 1, and were more likely to use visual cues to orient in test 2, compared with the other three groups. This paper demonstrates for the first time a cognitive dimorphism between sexes in an invertebrate. The data conform to the predictions of the range size hypothesis. Comparative studies with other invertebrate species might lead to a better understanding of the evolution of cognitive dimorphism.

**Keywords:** sexual maturation; spatial strategies; invertebrates; cephalopods

## 1. INTRODUCTION

Sex differences in cognitive abilities are the products of both individual life histories (e.g. influence of culture in humans) and differential evolutionary pressures (Geary 1995). Several evolutionary hypotheses have been proposed for such differences (Gaulin & FitzGerald 1989; Silverman *et al.* 2000; Jones *et al.* 2003; Ecuyer-Dab & Robert 2004). One of the best-supported hypotheses suggests that the sex differences in spatial abilities will evolve only in species where range expansion is significantly different between males and females (Gaulin & FitzGerald 1986, 1989). However, this hypothesis has substantial support only in rodents (see Jones *et al.* 2003). Since the basic demands of life appear quite similar in both vertebrates and invertebrates, we can hypothesize that similar ecological constraints in phylogenetically distant species could lead to the emergence of parallel cognitive sex differences to optimize reproductive success. Most cognitive studies in invertebrates do not indicate the sex of tested subjects and no study has reported cognitive sex differences in invertebrates.

Sex differences in spatial orientation have been well studied in a wide range of vertebrate species, including fishes (e.g. Sovrano *et al.* 2003), birds (e.g. Vallortigara 1996; Hodgson & Healy 2005), rodents (see Jonasson 2005) and humans (see Coluccia & Louse 2004). Although some studies have found no sex difference, or a difference favouring females (in humans: Postma *et al.* 1998; in rats: Healy *et al.* 1999), most have shown that males outperform females in a variety of spatial tasks (e.g. in meadow voles: in humans: Astur *et al.* 1998; Kavaliers *et al.* 1998). In many

species, males prefer to use spatial cues and females prefer conspicuous local cues (e.g. in chickens: Vallortigara 1996; in fishes: Sovrano *et al.* 2003; in rats: Blokland *et al.* 2006). In humans, male and female adults appear to employ different spatial strategies (Saucier *et al.* 2002) during way finding: Lawton (1994, 1996) and Lawton & Kallai (2002) found that females predominantly followed instructions about where to turn right or left whereas males predominantly relied on global reference points.

Cephalopod molluscs possess well-developed cognitive (see Mather 1995) and spatial abilities (for a review see Alves *et al.* 2007a; in octopuses: Mather 1991; Boal *et al.* 2000). Their behavioural repertoire is amazingly rich and with 200 million neurons, cephalopods have the largest and most complex nervous system of all invertebrates (see Nixon & Young 2003). The common cuttlefish (*Sepia officinalis*), a cephalopod mollusc, is a gonochoric species with a lifespan of less than 2 years. In the English Channel, cuttlefish reach sexual maturity between 14 and 20 months of age (Boucaud-Camou *et al.* 1991). Mating occurs several times in sexually mature cuttlefish, with intense competition among males for fertilization of females (Hanlon *et al.* 1999; Adamo *et al.* 2000). Consequently, we could hypothesize that, after sexual maturation, male cuttlefish navigate through a larger area compared with females, to maximize their number of potential mates, and this could have resulted in male-specific spatial abilities.

This study was designed to test this hypothesis. According to our prediction, sex differences would appear only after sexual maturation; consequently, experiments were conducted with sexually immature and mature cuttlefish of both sexes. First, an open field test was performed; the distances males and females travelled were compared to evaluate the likelihood of a difference in range

\* Author and address for correspondence: Groupe Mémoire et Plasticité comportementale, Université de Caen, 14032 Caen cedex, France (ludovic.dickel@unicaen.fr).

size. Indeed, in meadow voles (*Microtus pennsylvanicus*), the sex difference in spontaneous locomotor activity is consistent with field data on home range size (Perrot-Sinal *et al.* 1996). Second, spatial learning performances were assessed in a T-maze and the spatial strategy preferentially used by each cuttlefish was determined to evaluate whether males and females use different spatial orientation strategies. Alves *et al.* (2007b) showed that cuttlefish are able to solve a T-maze task using two kinds of strategy they either learn a motor response (right versus left turn) or orient using visual cues. In this study, potential sex differences were not assessed. We hypothesize that sexually mature male cuttlefish will travel further and will be more likely to use visual cues than sexually mature female cuttlefish or immature cuttlefish.

## 2. MATERIAL AND METHODS

### (a) Subjects

Sexually immature cuttlefish (9–11 cm dorsal mantle length) were trawled in the vicinity of Luc-sur-Mer (Calvados, France) between July and November 2006 and between July and September 2007. Sexually mature cuttlefish (18–22 cm dorsal mantle length) were trawled in the English Channel in February 2006 and were caught in basket traps in the vicinity of Granville (Manche, France) and Luc-Sur-Mer (Calvados, France) between April and June 2006. Cuttlefish were housed individually in glass tanks (80 × 50 × 50 cm<sup>3</sup>) with circulating seawater at 18 ± 1°C. The home tanks were maintained in a 12 L:12 D cycle (lights on at 08.30). Cuttlefish were fed either shrimp (*Crangon crangon*) or crabs (*Carcinus maenas*) once per day. They were allowed to acclimate in the laboratory for one week before behavioural experiments began.

Each cuttlefish was tested only once, either in the open field test or in the spatial learning task. In the open field test, four groups of cuttlefish were tested: Mi (sexually immature males, *n* = 6), Fi (sexually immature females, *n* = 13), Mm (sexually mature males, *n* = 28) and Fm (sexually mature females, *n* = 17). In the spatial learning task, four groups of cuttlefish were tested: Mi, Fi, Mm and Fm (*n* = 8 each). As there is no external sexual dimorphism before complete sexual maturation, the sex of immature cuttlefish was determined after completion of behavioural testing. Sexually immature cuttlefish were anaesthetized by placing them in seawater containing ethanol (2%) for 90 s, and quickly killed by decapitation. Subsequently, sex and stage of maturation were determined by examination of the gonads. Females were only included in the Fi group when nidamental glands were coloured white (an indicator of the first stage of sexual maturation, Richard 1971). For the males, the absence of spermatophores was the criterion of sexual immaturity.

### (b) Open field test

The open field apparatus consisted of a round tank made of white PVC, 1 m in diameter and 30 cm deep. The apparatus was filled to a depth of 15 cm with natural seawater, previously decanted, and lit by a 300 W halogen lamp positioned 1 m above the water surface. At the beginning of the test, each cuttlefish was gently removed from its home tank and placed in the centre of the open field. The distance travelled by cuttlefish in this apparatus was videotaped for 15 min with a digital video camera (3CCD DCR-TRV950E, Sony). To assist the analysis of the distance travelled, a

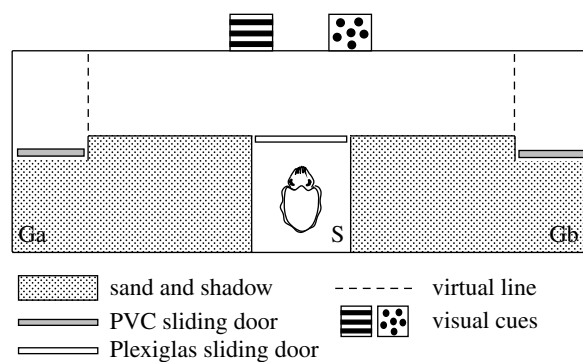


Figure 1. Schematic of the T-maze apparatus (not drawn to scale). Ga and Gb, goal compartments; S, start box.

transparent grid overlay was matched to the image of the video recordings on a TV screen. The number of squares (one square = 15 cm) traversed by each cuttlefish was counted. All tests were conducted between 09.00 and 12.00.

### (c) Spatial learning task

The apparatus (Alves *et al.* 2007b) consisted of a white plastic tank (200 cm long × 70 cm wide × 30 cm high) with internal divisions forming a T-maze (figure 1). The stem of the T (40 × 40 cm<sup>2</sup>) served as the start box (S) and the identical arms of the T (80 × 30 cm<sup>2</sup>) led to the goal compartments (Ca and Cb), situated at either side of the start box. The tank was filled to a depth of 30 cm with natural seawater maintained at a temperature of 18 ± 1°C. Both the goal compartments were darkened with an opaque sliding PVC top and the bottom of each goal compartment was completely covered with sand. Sliding doors allowed the cuttlefish to be confined either in the start box or in one of the goal compartments. Two visual cues were placed 5 cm above the water surface: a black-and-white striped PVC rectangle (15 cm high × 10 cm wide; stripes 3 cm wide) and a black-and-white spotted PVC square (15 cm wide; spots 3 cm in diameter). Black curtains were placed around and above the maze to eliminate visual cues around the apparatus. The tank was illuminated by a 100 W halogen lamp positioned 1 m above the water surface. Water was mixed and partially renewed between trials and totally renewed between training sessions.

In this maze, the cuttlefish learn how to enter a dark and sandy goal compartment to escape from the light. Cuttlefish were given five trials per training session, with one training session per day. During the first trial of the first session, both the goal compartments were closed to determine each cuttlefish's side-turning preference (see Alves *et al.* 2007b). During the remaining trials, only the goal compartment situated at the end of the arm not chosen during the first trial was open. During training trials, each cuttlefish was placed in the start box for 15 s before the Plexiglas sliding door to the maze alley was removed (figure 1). The cuttlefish was given a maximum of 5 min to reach the end of one arm. Each trial allowed only a single choice of direction (right or left arm). If the cuttlefish entered the incorrect arm and consequently failed to reach the goal compartment, it was immediately removed and replaced in the start box. Movement of any part of the cuttlefish beyond the virtual line at the far end of the incorrect arm was considered an error (figure 1). If the cuttlefish entered the correct arm and reached the goal compartment, then it remained in the dark, on the sandy bottom, for 15 min until the next trial. After that, it was

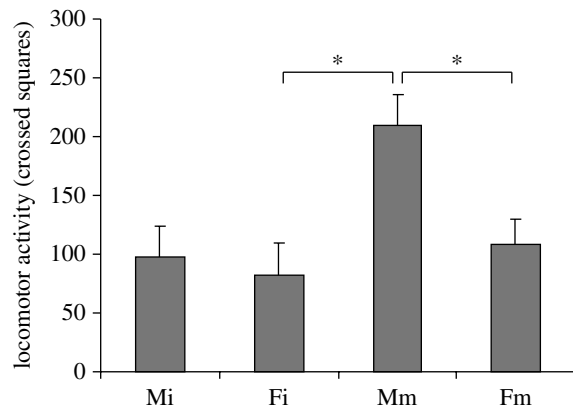


Figure 2. Locomotor activity of sexually immature males (Mi), immature females (Fi), mature males (Mm) and mature females (Fm) during the open field test, expressed in number of crossed squares. Error bars indicate standard errors of the mean. Asterisks indicate significant statistical difference with  $p < 0.05$  (Mann–Whitney test with sequential Bonferroni correction).

gently replaced in the start box with a net. The cuttlefish was replaced in its home tank between sessions. Training continued until the cuttlefish reached a learning criterion of 80% correct responses over two consecutive days of training (i.e. 8 correct choices out of 10). The day after reaching the learning criterion, the right/left positions of the two visual cues were reversed and both the goal compartments were opened. Then, the cuttlefish received one additional session of five trials. If the cuttlefish still consistently chose the arm rewarded during training (at least four choices out of five for the previously rewarded arm; same turning direction), then it used preferentially a motor response (right versus left turn) to find the goal compartment. However, if the cuttlefish chose the opposite arm (at least four choices out of five for the previously unrewarded arm; opposite turning direction), then it relied preferentially on visual cues to orient.

#### (d) Statistical analysis

All data were analysed with non-parametric tests (Siegel & Castellan 1988) and computed using STATXACT or SYSTAT software. Kruskal–Wallis tests were used to compare the distance travelled by Mi, Fi, Mm and Fm groups during the open field test and to make comparisons of the length of acquisition of the spatial learning task between the four groups. If the null hypothesis was rejected, we used Mann–Whitney tests for pairwise *post hoc* comparisons. Exact binomial tests were used to compare the spatial strategies within groups. Fisher's exact probability tests were used to determine whether there was a difference in spatial strategy between groups. For multiple comparisons,  $\alpha$  values were adjusted according to the sequential Bonferroni method as described by Holm (1979).

### 3. RESULTS

#### (a) Open field test

The Kruskal–Wallis test indicated that the distance travelled differed among the groups ( $n_{Mi}=6$ ;  $n_{Fi}=13$ ;  $n_{Mm}=28$ ;  $n_{Fm}=17$ ;  $H=13.71$ ;  $p=0.0033$ ). Pairwise comparisons showed that the distance travelled by Mm cuttlefish was significantly greater compared with the one travelled by the Fi and Fm cuttlefish (Mann–Whitney tests with sequential Bonferroni correction:  $n_{Mi}=6$ ;  $n_{Fi}=13$ ;

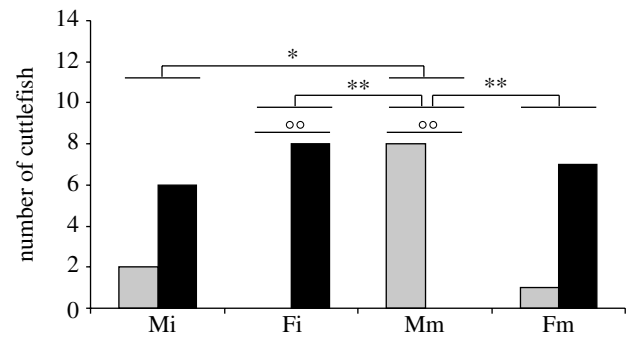


Figure 3. Number of cuttlefish relying on visual cues or on a motor response to orient when the right/left positions of the visual cues were reversed. Immature females (Fi) preferentially relied on a motor response and mature males (Mm) on visual cues (exact binomial test; double circles indicate significant statistical differences with  $p < 0.01$ ). Mature males (Mm) were significantly more likely to use visual cues than immature males (Mi), immature females (Fi) and mature females (Fm; Fisher's exact probability test with sequential Bonferroni correction; single and double asterisks indicate significant statistical difference with  $p < 0.05$  and  $p < 0.01$ , respectively). Grey bars, visual cues; black bars, motor response.

$n_{Mm}=28$ ;  $n_{Fm}=17$ ;  $Fi/Mm$ :  $U=71$ ;  $p=0.002$ ;  $Fm/Mm$ :  $U=126$ ;  $p=0.009$ ; figure 2).

#### (b) Spatial learning task

Mi and Fi cuttlefish reached the learning criterion in a mean of 6 sessions (range, 3 to 14 sessions). Mm and Fm cuttlefish reached the learning criterion in a mean of 6 sessions (range, 3 to 12 sessions). No difference in acquisition length (number of sessions to reach the acquisition criterion) was observed between the groups (Kruskal–Wallis test:  $n_{Mi}=8$ ;  $n_{Fi}=8$ ;  $n_{Mm}=8$ ;  $n_{Fm}=8$ ;  $H=1.812$ ;  $p=0.612$ ).

During the probe session, all Fi cuttlefish used a motor response (right versus left turn; exact binomial test:  $Fi$ :  $p=0.008$ ; figure 3). Seven out of eight Fm cuttlefish and six out of eight Mi cuttlefish tested relied on a motor response (exact binomial test:  $Fm$ ,  $p=0.070$ ;  $Mi$ ,  $p=0.289$ ). By contrast, all Mm cuttlefish relied on visual cues (exact binomial test:  $p=0.008$ ; figure 3). Mm cuttlefish were significantly more likely to use visual cues than Mi, Fi and Fm cuttlefish (Fisher's exact probability test with sequential Bonferroni correction:  $n_{Mi}=8$ ;  $n_{Fi}=8$ ;  $n_{Mm}=8$ ;  $n_{Fm}=8$ ;  $Fi/Mm$ ,  $p=0.0001$ ;  $Mi/Mm$ ,  $p=0.0035$ ;  $Fm/Mm$ ,  $p=0.0007$ ; figure 3).

### 4. DISCUSSION

As predicted, sexually mature male cuttlefish travelled further and were more likely to use visual cues than sexually mature or immature female cuttlefish. We were unable to draw conclusions about distance travelled for immature males owing to our small sample size. Interestingly, our study revealed similar rates of acquisition (i.e. same number of sessions to reach the learning criterion) in solving the spatial task for both sexes and stages of sexual maturation. There was a difference between mature males and the other three groups only in the strategy used to solve the maze. Mature males preferred to use visual cues while



the other three groups preferred to rely on motor responses (right versus left turn).

Our data are consistent with the predictions of the range size hypothesis (Gaulin & FitzGerald 1986, 1989): a difference in range expansion between males and females is associated with a difference in spatial learning abilities. The results of the open field test suggest a greater propensity for exploring new environments by males than females. In rodents, some of the data that support the range size hypothesis are equally consistent with the fertility and parental care hypothesis (Jones *et al.* 2003), which states that female reproductive success is enhanced by reduced mobility during reproductive periods (Sherry & Hampson 1997). In cuttlefish, it is clear that the difference between adult males and females resulted from an increase in mobility in males rather than a decrease in mobility of females during reproductive period since the activity of immature males and females was similar to that of mature females. Field studies are needed to confirm the range size hypothesis in cuttlefish: are males navigating in a larger area to maximize the number of potential mates?

Gonadal hormones can have important organizational and activational effects on sexually dimorphic spatial abilities in rodents and birds (Kritzer *et al.* 2001; Isgor & Sengelaub 2003). In particular, sex steroids, such as oestradiol and testosterone, are known to influence locomotor activity and spatial learning in mammals. In meadow voles, a positive relationship has been demonstrated between testosterone and locomotor activity levels (Perrot-Sinal *et al.* 1998), with higher testosterone levels associated with larger home range (Turner *et al.* 1983). However, the variations of oestrogen levels across the oestrous cycle of females complicate comparisons of spatial performances of males and females (Healy *et al.* 1999). The absence of a reproductive cycle in cuttlefish could be an advantage for the study of the endocrine basis of sex differences in cognition. Oestradiol and testosterone have been described in cephalopods (*Octopus vulgaris*; D'Aniello *et al.* 1996); the possible roles of oestradiol and testosterone in the sex differences in locomotor activity and cognitive ability of cuttlefish remain to be determined.

Sexual dimorphisms in key areas of the central nervous system have also been suggested to underlie sex differences in spatial orientation (Jacobs *et al.* 1990; Kavaliers *et al.* 1998). In rodents, the hippocampus is important only in spatial strategies that use several extra-maze cues (Packard & McGaugh 1996; Teather *et al.* 2005). Jacobs *et al.* (1990) showed that in meadow voles, males have a larger hippocampus when compared with that of females, but only in the species displaying sex differences in spatial learning (e.g. *Microtus pennsylvanicus* and not *Microtus pinetorum*). Data are still scarce concerning the neural substrates underlying spatial learning in cephalopods. The vertical lobe of the cuttlefish brain is known to share cellular processes (long-term potentiation, Hochner *et al.* 2003) and structural (sequences of intersected matrices, Young 1991) and functional properties (implication in locomotor activity level and memory, Graindorge *et al.* 2006) with the hippocampus. Electrolytic lesions of the ventral part of the vertical lobe induced impairments in the acquisition of a comparable spatial task (Graindorge *et al.* 2006). Thus, it would be interesting to undertake

comparative studies of the vertical lobe between males and females.

In mammals, several authors have demonstrated that strategies that use several extra-maze cues develop after simpler strategies, such as orienting to a proximal cue or repeating the same sequence of movements (rats: Rudy *et al.* 1987; humans: Laurance *et al.* 2003). The slower maturation of the hippocampus is considered to be responsible for this later appearance of complex spatial strategies. In our study, the preference for using visual cues appears in males after sexual maturation. The vertical lobe of the cuttlefish brain matures late in post-embryonic development (Dickel *et al.* 2001) and could possibly be responsible for the later maturation of the cue-based strategy compared with the motor response-based strategy.

To our knowledge, our study is the first to demonstrate a sex difference in the cognitive abilities in an invertebrate. Our results clearly demonstrate the necessity for future studies of cognition in cephalopods to consider the sex and level of sexual maturation of tested animals. Studying the physiological and environmental factors underlying such cognitive differences in cuttlefish will provide valuable information towards understanding the evolution of sex differences in cognitive abilities.

The experiments complied with French animal testing laws.

We thank John O'Brien, Vincent Viblanc and two anonymous reviewers for their helpful comments on a previous version of the manuscript. We also thank the CREC staff for their technical assistance and the INSU-CNRS for providing cuttlefish. This work was supported by a grant from the Ministère de l'Enseignement Supérieur et de la Recherche to C.J.-A.

## REFERENCES

- Adamo, S. A., Brown, W. M., King, A. J., Mather, D. L., Mather, J. A., Shoemaker, K. L. & Wood, J. B. 2000 Agonistic and reproductive behaviours of the cuttlefish *Sepia officinalis* in a semi-natural environment. *J. Mollus. Stud.* **66**, 417–419. (doi:10.1093/mollus/66.3.417)
- Alves, C., Boal, J. G. & Dickel, L. 2007a Short-distance navigation in cephalopods: a review and synthesis. *Cogn. Proc.* (doi:10.1007/s10339-007-0192-9).
- Alves, C., Chichery, R., Boal, J. G. & Dickel, L. 2007b Orientation in the cuttlefish *Sepia officinalis*: response versus place strategy. *Anim. Cogn.* **10**, 29–36. (doi:10.1007/s10071-006-0027-6)
- Astur, R. S., Ortiz, M. L. & Sutherland, R. J. 1998 A characterization of performance by men and women in a virtual Morris water task: a large and reliable sex difference. *Behav. Brain Res.* **93**, 185–190. (doi:10.1016/S0166-4328(98)00019-9)
- Blokland, A., Rutten, K. & Prickaerts, J. 2006 Analysis of spatial orientation strategies of male and females Wistar rats in a Morris water escape task. *Behav. Brain Res.* **171**, 216–224. (doi:10.1016/j.bbr.2006.03.033)
- Boal, J. G., Dunham, A. W., Williams, K. T. & Hanlon, R. T. 2000 Experimental evidence for spatial learning in octopuses (*Octopus bimaculoides*). *J. Comp. Psychol.* **114**, 246–252. (doi:10.1037/0735-7036.114.3.246)
- Boucaud-Camou, E., Koueta, N., Boismery, J. & Medhioub, A. 1991 The sexual cycle of *Sepia officinalis* L. from the Bay of Seine. In *La seiche, the cuttlefish* (ed. E. Boucaud-Camou), pp. 141–151. Caen, France: Centre de Publications de l'Université de Caen.

- Coluccia, E. & Louse, G. 2004 Gender differences in spatial orientation: a review. *J. Environ. Psychol.* **24**, 329–340. (doi:10.1016/j.jenvp.2004.08.006)
- D'Aniello, A., Di Cosmo, A., Di Cristo, C., Assisi, L., Botte, V. & Di Fiore, M. M. 1996 Occurrence of sex steroids hormones and their binding proteins in *Octopus vulgaris* Lam. *Biochem. Biophys. Res. Commun.* **227**, 782–788. (doi:10.1006/bbrc.1996.1585)
- Dickel, L., Chichery, M. P. & Chichery, R. 2001 Increase of learning abilities and maturation of the vertical lobe complex during postembryonic development in the cuttlefish, *Sepia*. *Dev. Psychobiol.* **39**, 92–98. (doi:10.1002/dev.1033)
- Ecuyer-Dab, I. & Robert, M. 2004 Have sex differences in spatial abilities evolved from male competition for mating and female concern for survival? *Cognition* **91**, 221–257. (doi:10.1016/j.cognition.2003.09.007)
- Gaulin, S. J. C. & FitzGerald, R. W. 1986 Sex differences in spatial ability: an evolutionary hypothesis and test. *Am. Nat.* **127**, 74–88. (doi:10.1086/284468)
- Gaulin, S. J. C. & FitzGerald, R. W. 1989 Sexual selection for spatial-learning ability. *Anim. Behav.* **37**, 322–331. (doi:10.1016/0003-3472(89)90121-8)
- Geary, D. C. 1995 Sexual selection and sex differences in spatial cognition. *Learn. Individ. Differ.* **7**, 289–301. (doi:10.1016/1041-6080(95)90003-9)
- Graindorge, N., Alves, C., Darmaillacq, A. S., Chichery, R., Dickel, L. & Bellanger, C. 2006 Effects of dorsal and ventral vertical lobe electrolytic lesions on spatial learning and locomotor activity in *Sepia officinalis*. *Behav. Neurosci.* **120**, 1151–1158. (doi:10.1037/0735-7044.120.5.1151)
- Hanlon, R. T., Ament, S. A. & Gabr, H. 1999 Behavioral aspects of sperm competition in cuttlefish, *Sepia officinalis* (Sepioidea: Cephalopoda). *Mar. Biol.* **134**, 719–728. (doi:10.1007/s002270050588)
- Healy, S. D., Braham, S. R. & Braithwaite, V. A. 1999 Spatial working memory in rats: no differences between the sexes. *Proc. R. Soc. B* **266**, 2303–2308. (doi:10.1098/rspb.1999.0923)
- Hochner, B., Brown, E. R., Langella, M., Shomrat, T. & Fiorito, G. 2003 A learning and memory area in the octopus brain manifests a vertebrate-like long-term potentiation. *J. Neurophysiol.* **90**, 3547–3554. (doi:10.1152/jn.00645.2003)
- Hodgson, Z. G. & Healy, S. D. 2005 Preference for spatial cues in a non-storing songbird species. *Anim. Cogn.* **8**, 211–214. (doi:10.1007/s10071-004-0249-4)
- Holm, S. 1979 A simple sequentially rejective multiple test procedure. *Scand. J. Statist.* **6**, 65–70.
- Isgor, C. & Sengelaub, D. R. 2003 Effects of neonatal gonadal steroids on adult CA3 pyramidal neuron dendritic morphology and spatial memory in rats. *J. Neurobiol.* **55**, 179–190. (doi:10.1002/neu.10200)
- Jacobs, L. F., Gaulin, S. J. C., Sherry, D. F. & Hoffman, G. E. 1990 Evolution of spatial cognition: sex-specific patterns of spatial behaviour predict hippocampal size. *Proc. Natl Acad. Sci. USA* **87**, 6349–6352. (doi:10.1073/pnas.87.16.6349)
- Jonasson, Z. 2005 Meta-analysis of sex differences in rodent models of learning and memory: a review of behavioral and biological data. *Neurosci. Biobehav. Rev.* **28**, 811–825. (doi:10.1016/j.neubiorev.2004.10.006)
- Jones, C. M., Braithwaite, V. A. & Healy, S. D. 2003 The evolution of sex differences in spatial ability. *Behav. Neurosci.* **117**, 403–411. (doi:10.1037/0735-7044.117.3.403)
- Kavaliers, M., Ossenkopp, K. P., Galea, L. A. M. & Kolb, B. 1998 Sex differences in spatial learning and prefrontal and parietal cortical dendritic morphology in the meadow vole, *Microtus pennsylvanicus*. *Brain Res.* **810**, 41–47. (doi:10.1016/S0006-8993(98)00868-3)
- Kritzer, M. F., McLaughlin, P. J., Smirlis, T. & Robinson, J. K. 2001 Gonadectomy impairs T-maze acquisition in adult male rats. *Horm. Behav.* **39**, 167–174. (doi:10.1006/hbeh.2001.1645)
- Laurance, H. E., Learmonth, A. E., Nadel, L. & Jacobs, J. 2003 Maturation of spatial navigation strategies: convergent findings from computerized spatial environments and self-report. *J. Cogn. Dev.* **4**, 211–238. (doi:10.1207/S15327647JCD0402\_04)
- Lawton, C. A. 1994 Gender differences in way-finding strategies: relationship to spatial ability and spatial anxiety. *Sex Roles* **30**, 765–779. (doi:10.1007/BF01544230)
- Lawton, C. A. 1996 Strategies for indoor wayfinding: the role of orientation. *J. Environ. Psychol.* **16**, 137–145. (doi:10.1006/jevp.1996.0011)
- Lawton, C. A. & Kallai, J. 2002 Gender differences in wayfinding strategies and anxiety about wayfinding: a cross-cultural comparison. *Sex Roles* **47**, 389–401. (doi:10.1023/A:1021668724970)
- Mather, J. 1991 Navigation by spatial memory and use of visual landmarks in octopuses. *J. Comp. Physiol. A* **168**, 491–497. (doi:10.1007/BF00199609)
- Mather, J. 1995 Cognition in cephalopods. In *Advances in the study of behavior*, vol. 24 (eds P. J. B. Slater, J. S. Rosenblatt & C. T. Snowdon), pp. 317–353. San Diego, CA: Academic Press.
- Nixon, M. & Young, J. Z. 2003 *The brains and lives of cephalopods*. Oxford, UK: Oxford University Press.
- Packard, M. G. & McGaugh, J. L. 1996 Inactivation of hippocampus or caudate nucleus with lidocaine differentially affects expression of place and response learning. *Neurobiol. Learn. Mem.* **65**, 65–72. (doi:10.1006/nlme.1996.0007)
- Perrot-Sinal, T. S., Heale, V. R., Ossenkopp, K. P. & Kavaliers, M. 1996 Sexually dimorphic aspects of spontaneous activity in meadow voles (*Microtus pennsylvanicus*): effects of exposure to fox odor. *Behav. Neurosci.* **110**, 1126–1132. (doi:10.1037/0735-7044.110.5.1126)
- Perrot-Sinal, T. S., Innes, D., Kavaliers, M. & Ossenkopp, K. P. 1998 Plasma testosterone levels are related to various aspects of locomotor activity in wild-caught male meadow voles (*Microtus pennsylvanicus*). *Physiol. Behav.* **64**, 31–36. (doi:10.1016/S0031-9384(98)00015-8)
- Postma, A., Izendoorn, R. & De Haan, E. H. F. 1998 Sex differences in object location memory. *Brain Cogn.* **36**, 334–345. (doi:10.1006/brcg.1997.0974)
- Richard, A. 1971 Contribution à l'étude expérimentale de la croissance et de la maturation sexuelle de *Sepia officinalis* L. (Mollusque, Céphalopode). Thèse de doctorat d'état, Université de Lille.
- Rudy, J. W., Staedler-Morris, S. & Albert, P. 1987 Ontogeny of spatial navigation behaviors in the rat: dissociation of “proximal” and “distal” cue-based behaviors. *Behav. Neurosci.* **101**, 62–73. (doi:10.1037/0735-7044.101.1.62)
- Saucier, D. M., Green, S. M., Leason, J., MacFadden, A., Bell, S. & Elias, L. J. 2002 Are sex differences in navigation caused by sexually dimorphic strategies or by differences in the ability to use the strategies? *Behav. Neurosci.* **116**, 403–410. (doi:10.1037//0735-7044.116.3.403)
- Sherry, D. F. & Hampson, E. 1997 Evolution and the hormonal control of sexually-dimorphic spatial abilities in humans. *Trends Cogn. Sci.* **1**, 50–56. (doi:10.1016/S1364-6613(97)01015-2)
- Siegel, S. & Castellan, N. J. 1988 *Nonparametric statistics for the behavioral sciences*, 2nd edn. New York, NY: McGraw-Hill.
- Silverman, I., Choi, J., Mackewn, A., Fisher, M., Moro, J. & Olshansky, E. 2000 Evolved mechanisms underlying wayfinding: further studies on the hunter-gatherer-theory of spatial sex differences. *Evol. Hum. Behav.* **21**, 201–213. (doi:10.1016/S1090-5138(00)00036-2)

- Sovrano, V. A., Bisazza, A. & Vallortigara, G. 2003 Modularity as a fish (*Xenotoca eiseni*) views it: conjoining geometric and nongeometric information for spatial reorientation. *J. Exp. Psychol. Anim. Behav. Process.* **29**, 199–210. (doi:10.1037/0097-7403.29.3.199)
- Teather, L. A., Packard, M. G., Smith, D. E., Ellis-Behnke, R. G. & Bazan, N. G. 2005 Differential induction of c-Jun and Fos-like proteins in rat hippocampus and dorsal striatum after training in two water maze tasks. *Neurobiol. Learn. Mem.* **84**, 75–84. (doi:10.1016/j.nlm.2005.03.006)
- Turner, B. N., Iverson, S. L. & Severson, K. L. 1983 Seasonal changes in open-field behavior in wild male meadow voles (*Microtus pennsylvanicus*). *Behav. Neural Biol.* **39**, 60–77. (doi:10.1016/S0163-1047(83)90637-4)
- Vallortigara, G. 1996 Learning of colour and position cues in domestic chicks: males are better at position, females at colour. *Behav. Process.* **36**, 289–296. (doi:10.1016/0376-6357(95)00063-1)
- Young, J. Z. 1991 Computation in the learning system of cephalopods. *Biol. Bull.* **180**, 200–208. (doi:10.2307/1542389)